HAPLOPAPPUS CRISPUS AND H. ZIONIS (ASTERACEAE): NEW SPECIES FROM UTAH

Loran C. Anderson¹

ABSTRACT. — The new species, $Haplopappus\ crispus\$ and $H.\ zionis\$ of section Macronema, are formally described and illustrated. They are endemic to southern Utah. Also, $H.\ bloomeri\$ ssp. $compactus\$ is raised to species. Chromosome numbers of all three are n=9. Aspects of anatomy are detailed. Comparisons are made to $H.\ bloomeri\$ and $H.\ suffruticosus\$. Relationships are discussed, and a key to the species is given.

The only comprehensive monograph of *Haplopappus* is that of H. M. Hall (1928). In recent years the generic integrity of *Haplopappus* has been questioned (see Anderson 1980 for review). Data from anatomy, cytology, and chemistry suggest it is a polyphyletic assemblage. Nevertheless, a suitable taxonomic reorganization of the group has not been achieved. Therefore, I choose to describe new taxa under the name *Haplopappus* even though the species will very probably be placed in some other genus at a later date.

Some years ago 1 found plants in southern Utah that appeared to be *H. bloomeri* Gray ssp. compactus Hall; a chromosome count for the collection, Anderson 3358, was published under that name (Anderson et al. 1974). Other collectors had identified similar plants as *H. suffruticosus* (Nutt.) Gray. The combined collections actually represent two new species of section Macronema, and, additionally, *H. bloomeri* ssp. compactus should be elevated to species level.

METHODS AND MATERIALS

Fresh and dried materials were processed for anatomical study as in Anderson (1970a). Five heads from personal collections, along with one to five heads from other collections, were measured (as in Anderson 1964) for involucral and floral data. Cytological methods are those of Anderson (1966).

Voucher specimens for anatomical (a) and morphological (m) studies are: *H. bloomeri*: *Anderson 1620*, m (FSU), *Anderson 2018*, a and m (FSU), *Anderson 2943*, a (FSU), *Anderson 4539*, m (FSU), *Reveal 1070*, m (FSU); *H.*

compactus: Ackerman 30797, m (FSU), Anderson 6186, a and m (FSU), Clokey 8570, m (UTC); H. crispus: Anderson 5504, a and m (FSU), Cottam 1526, m (BRY), Maguire 13386, m (UTC), Stanton in 1927, m (BRY); H. suffruticosus: Anderson 1023, m (FSU), Anderson 2920, a (FSU), Anderson 2970, a and m (FSU), Goodrich 10133, m (BRY), Shultz 3738, m (UTC), Yoder-Williams 1311, a (FSU), Wiggins 9298, m (UTC); and H. zionis: Anderson 3358, m (FSU), Anderson et al. 5094, a and m (FSU), Arnow 107, m (UT).

TAXONOMY

Haplopappus compactus (Hall) L. C. Anderson, comb. nov.

Basionym: Haplopappus bloomeri Gray ssp. compactus Hall. Carnegie Inst. Publ. 389:199, fig. 68, 1928. Type. — Nevada: Clark Co., Charleston [Spring] Mountains, E. C. Jaeger on 12 Sep 1925 (holotype: POM!; isotype: UC!).

Synonymy: *Haplopappus bloomeri* Gray var. *compactus* (Hall) Blake in Clokey. Univ. Calif. Publ. Bot. 24:231, 1951.

The only description of this taxon is that given by Hall (1928). It is amplified and emended with the following: woody shrubs to 5 dm tall; leaves oblanceolate-spatulate, 2–3.5(4) cm long, (2)2.5–3(5) mm wide; heads (involucres) 12–14.8 mm long, 4.5–5.5 mm wide, phyllaries 18–24; disk flowers 11–16, golden yellow (fading lighter), corollas 9.1–11.4 mm long, tubes glandular, strongly dilated at point of staminal departure (at 50 percent of total corolla length), lobes 0.8–1.6 mm long, styles 12.5–14.5 mm long.

Department of Biological Science, Florida State University, Tallahassee, Florida 32306.

In addition to specimens cited by Hall (1928) and Clokey (1951), the following represent this species: NEVADA: Clark Co., above McWilliams Campground at 8500 ft, Lee Canyon, Spring Mountains, L. C. Anderson 6186 (BRY, FSU, UNLV, UTC), A. D. Blauer & E. D. McArthur N-144, N-145 (FSU, SSLP), W. E. Niles 3160 (FSU, UNLV); top of ridge, Charleston Mountain, 11,500 ft, T. Dawson 7 (UC); top of Sheep Mountains, 9300 ft, T. L. Ackerman 30797 (FSU, NY).

The last collection is a range extension for *H. compactus*; the taxon was previously thought to be endemic to the Spring (or Charleston) Mountains.

Haplopappus crispus L. C. Anderson, sp. nov.

Frutices lignosi 3-4(5) dm alti; caules foliosi, graciles, erecti, tenuiter glandulosi; folia spatulata vel oblanceolata et acuminata, marginibus undulatis et crispis, (1.5)2-2.5(30) cm longa, (3)5-6(8) mm lata, in ramis altioribus solum parvo minora; inflorescentia cyma solute paniculata vel aliquanto congesta, temporibus paucis solum uno capitulo vel duobus capitula ramum; campanulata, (12.5)13-14(15) mm longa, (5)6.5-7(9) mm lata, foliis superioribus saepissime separata; phyllaria (24)26-30(35); nulli radii flosculi; disci flosculi (14)15-20(24), luridi, corollis (9.5)10-10.8 mm longis, tubulo aliquanto dilato, lobis 1-1.5 mm longis, stylis 14-18 mm longis, lineis stigmaticis multo brevioribus quam appendicibus; achenia 6.5-8.5 mm longa et raro pubescentia.

Type.— Utah: Washington Co., weathered andesite with manzanita in mountain mahogany-fir woods with few pine and aspen along Whipple Valley Trail at 8100 ft, above Pine Valley, 19 air mi NE of St. George in Pine Valley Mountains, T39S, R14W, E1/2 Sec 29, 18 Sep 1981, L. C. Anderson 5504 (holotype: BRY; isotypes: FSU, MO, NY, RSA, UC, UTC).

Woody shrubs, much branched at base, 3–4(5) dm tall (or taller?); leafy stems slender, erect, covered with short-stalked glands; leaves entire, alternate, green, spatulate to oblong-oblanceolate, acuminate, margins wavy-crispate, glutinous with low glands (not prominently stalked as in *H. suffruticosus*), (1.5)2–2.5(3) cm long, (3)5–6(8) mm wide,

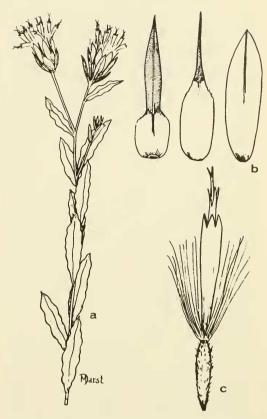


Fig. 1. Haplopappus crispus (Anderson 5504): a., flowering branch with crispate leaves and rather naked peduncles; b., involucral bracts, outermost with large green tips, inner ones with narrowed tips, innermost without green tips; c., disk flower with gradually flaring corolla and sparsely strigose achenes. A., x 1; b. and c., x 4.

only slightly reduced toward the inflorescence, but generally not crowding the heads as in H. zionis; inflorescence a loosely paniculate to somewhat congested cyme, occasionally reduced to one or two heads per branch (Fig. 1a); heads campanulate, (12.5)13-14(15) mm long, (5)6.5-7(9) mm wide; phyllaries (24)26-30(35), 1-nerved, finely glandular, outermost bracts mostly green, leaflike, inner bracts stramineous, abruptly or gradually narrowed into a slender green tip, innermost bracts stramineous, erose-ciliate apically, but not as pronounced as in H. zionis; ray flowers absent; disk flowers (14)15-20(24), pale yellow, corollas (9.5)10-10.8 mm long, tubes glandular pubescent, not abruptly dilated as in H. compactus and H. zionis, lobes 1-1.5 mm long,

styles 14–18 mm long, branches slender, stigmatic lines much shorter than appendages (22–36 percent of total branch length); achenes cylindric, 6.5–8.5 mm long, sparsely but evenly pubescent, pappus 8–9.5 mm long; n = 9. Infrequent, generally in moderately open settings in spruce-pine associations, (3000?) 8100–10,000 ft, apparently endemic to mountains of southwestern Utah. August-September.

ADDITIONAL SPECIMENS EXAMINED.— Utah: Millard Co., Pine Valley, W. D. Stanton in 1927 (BRY); Washington Co., south end Pine Valley Mountains, 9200 ft, B. Albee 2911a (UT), Anderson Valley area, north end Pine Valley Mountains, 8400 ft, B. Albee 2911b (UT), Pine Valley Mountains, T39S, R14W, J. L. Gentry & E. Jensen, Jr., 2245 (BRY, NY, UTC), R. K. Gierisch 542 (UC, UTC), Pine Valley Mountains, 8500 ft, W. P. Cottam 5699 (UT), 10,000 ft, B. Maguire & B. L. Richards, Jr., 13386 (UC, UTC), Santa Clara, 3000 ft, W. P. Cottam 1526 (BRY, NY, UT). The last collection is so far out of range altitudinally that it may represent a chance introduction; the population has not been found again to determine its persistence. The collection is of further interest for the notation "along ditch banks, 8-10 ft tall"; also, it has heads with greater numbers of phyllaries and flowers than the other collections.

Haplopappus zionis L. C. Anderson, sp. nov. Frutices humiles et diffundentes 1-3 dm alti; corpulenti caules decumbentes vel ascendentes, foliosi in inflorescentiam et glandulosi-hispiduli; folia spatulata et acuminata, (2.5)3-3.5(4) cm longa, 2.4-4(7) mm lata; inflorescentia cyma paniculata et congesta et foliosa; capitula turbinata vel anguste campanulata, (14)16-19(22) mm longa, 6-8 mm lata, bracteis exterioribus in forma folii apicibus longis et acuminatis, interioribus apice villosis, phyllariis (17)20-22(23); nulli radii flosculi; disci flosculi (10)12-18(21), flavi, corollis (9.5)9.8-10.8(11.5) mm longis, tubulis subito dilatis, lobis 1.2-2 mm longis, stylis 18-19 mm longis, lineis stigmaticis multo brevioribus quam appendicibus; achenia 7-8 mm longa et ferme glabra.

Type.— Utah: Iron Co., moderately bare, weathered pink limestone member of Wasatch Formation in aspen, spruce, limber

pine, bristlecone pine association near top of Cedar Canyon, 9800 ft, 13.5 air mi SE of Cedar City, 30 Aug 1980, *L. C. Anderson*, S. *L. Welsh*, and M. Chatterley 5094 (holotype: BRY; isotypes: ASU, DS, FSU, MO, NY, RSA, UC, UTC).

Low, branching, spreading shrubs, 1-3 dm tall; stems stout, decumbent or ascending, glandular-hispidulous, leafy into the inflorescence (Fig. 2a); leaves entire, alternate, green, spatulate, acuminate, margins not undulate or crispate, glandular but less glutinous than H. crispus, (2.5)3-3.5(4) cm long, 2.5-4(7) mm wide; inflorescence a congested, leafy paniculate cyme; heads turbinate to narrowly campanulate, (14)16-19(22) mm long, 6-8 mm wide, lateral heads fewer flowthan central ones; phyllaries (17)20-22(23), 3-nerved, finely glandular, outermost bracts leaflike and much longer than other bracts, inner bracts stramineous with long green tips, innermost bracts stramineous with praemorse, prominently villous tips (Fig. 2b); ray flowers absent; disk flowers (10)12-18(21), golden yellow, corollas (9.5)9.8-10.8(12) mm long, tubes abruptly dilated at point of staminal departure (at 40 percent of total corolla length), sparsely glandular, lobes 1.2-2 mm long, styles 18-19 mm long, branches slender, stigmatic lines much shorter than appendages (23-31 percent of total branch length); achenes cylindric, 7-8 mm long, essentially glabrous with few hairs apically (Fig. 2c), pappus 9-9.5 mm long; n = 9. Infrequent, usually on gravelly sandy clay from limestones, often with manzanita on rather barren slopes in spruce, fir, pine associations, 8,000-10,000 ft, apparently endemic to mountains of southern Utah. July-September.

Additional specimens examined: Utah, Garfield County, vic. summit between Escalante and Widtsoe, Escalante Mountains, 9000 ft, W. P. Cottam 6562 (UT), 9100 ft, L. C. Anderson 3358 (BRY, FSU, KSC, NY, UC, UTC), 10,000 ft, E. Neese & S. White 3964 (BRY), 2 miles south of Pine Lake, Escalante Mountains, E. Neese & S. White 3844; Iron County, Cedar Canyon, southeast of Cedar City, 8000 ft, L. Arnow 107 (UT), R. Foster 5297 (BRY), vic. Midway Summit, west of Cedar Breaks, 10,000 ft, B. Maguire & B. L.

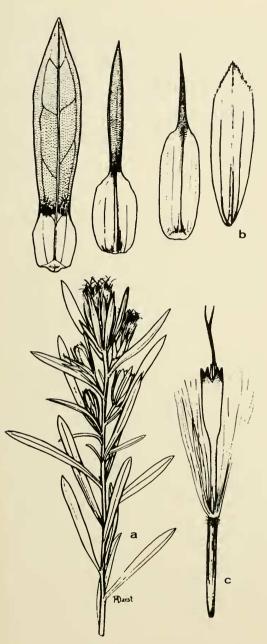


Fig. 2. Haplopappus zionis (Anderson et al. 5094): a., flowering branch with foliage overtopping flowering heads; b., involucral bracts, outermost leaflike and 3-nerved, inner ones with elongate green tips, innermost with prominently villous tip; c., disk flower with abruptly dilated corolla tube, long style, and nearly glabrous achene with very few hairs just below pappus. a., x 1; b. and c., x 4.

Richards, Jr. 13389 (UTC); Co. unknown, Dixie National Forest, R. K. Gierisch 217 (UTC).

CYTOLOGY AND ANATOMY

Chromosome numbers of section Macronema of *Haplopappus* are monotonously uniform at n = 9 with an apparent absence of polyploidy and aneuploidy (Anderson et al. 1974). The new species are also n = 9. Original counts for *H. compactus* and *H. crispus* were made from root tip squashes from *Niles 3160* and *Anderson 5504*, respectively. An earlier count for *H. zionis* (Anderson 3358) was listed as *H. bloomeri* ssp. compactus in Anderson et al. (1974).

Meiotic behavior has not been observed for any of the new species, but all three have pollen fertilities above 98 percent (as determined by staining in cotton blue in lactophenol). Embryo sac development appears normal (Polygonum type) in *H. compactus*, *H. crispus*, and *H. suffruticosus*; it was not studied in *H. bloomeri* and *H. zionis*. Mature embryo sacs are long and narrow (280–380 µm long) and 8-nucleate without multiplication of antipodals as found in many *Chrysothamnus* (Anderson 1970b).

Aspects of floral anatomy for the new species and possibly related taxa are summarized in Table 1 (following format in Anderson 1970a); frequency categories are: ++, abundant; +, frequent; -, rare; and 0, absent. General information on the other taxa of Haplopappus is in Nelson (1982). Achenes of H. zionis have the greatest amount of vasculature, whereas those of H. crispus have the least. Secretory canals vary from abundant to absent at selected levels in the achenes and corollas. They are always absent in the styles of these species but present in H. macronema (Anderson 1970a).

Achenes of *H. bloomeri*, *H. compactus*, and *H. zionis* are essentially glabrous but with a few twin hairs just below the pappus attachment (the last being the "most glabrous"). A few short glandular trichomes (60–66 μ m long) are hidden among the abundant twin hairs on *H. suffruticosus* achenes, and larger glandular hairs (190 μ m) occur rarely on achenes of *H. bloomeri*. Glandular trichomes on achenes were so rare that they were omitted from Table 1, and they do not occur in the new species. Pappus bristles are positioned in three closely spaced rows on achenes of *H. zionis* and in two in the other four

Table 1. Comparisons for range and aspects of morphology of selected taxa of Haplopappus, section Macronema.

	H. bloomeri	H. compactus	H. crispus	H. suffruticosus	H. zionis
Range	Calif., W Nev.,	S Nev.	SW Utah	Calif., Nev., Idaho,	S Utah
3	Oregon, S Wash.			W Wyo., SW Mont.	
Elevation, ft	3500-9600	7900-11,500	(3000)8100-10,000	7500-12,300	8000-10,000
Habit of growth	tall, 4-5 dm	tall, 4–5 dm	medium, 3-4 dm	low, 1-3 dm	low, 1-3 dm
Leaf size, cm x mm	$2-6 \times 0.5-3$	2-4 x 2-5	1.5-3 x 3-8	1-3 x 1.5-5	2.5-4 x 2.5-7
Leaf shape	filiform-narrowly	oblanceolate-	spatulate-	oblong-spatulate	spatulate
	oblanceolate	spatulate	oblanceolate		
Leaf margins	smooth	smooth	crispate	crispate	smooth
Head length, mm	7.8-12.2(16)	12-15	12.5-15	8-16	14-22
Head width/length ratio	.2935	.3640	.4548	.4560	.3841
Phyllary number	17-36	18-24	24-35	17-31	17-23
Ray flower number	(0)1-3	0	0	(0)1-8	0
Disk flower number	4-8(12)	11-16	14-24	15-40	10-21
Disk flower length, mm	7.3-9.4(10.9)	9.1-11.4	9.5 - 10.8	8.5-11	9.5-12
Corolla tube	straight	dilated	\pm dilated	straight	dilated
Corolla lobe length, mm	0.9-1.9	0.8 - 1.6	1.0-1.5	1.0 - 1.7	1.2 - 2.0
Style branch, mm	2.5-4.3	3.8-4.4	3.8-4.8	2.6-4.6	4.2 - 5.2
Achene length, mm	6-7	7.5-8.5	6.5-8.5	7.5-8	7-8
Achene pubescence	glabrous	glabrous	sparsely strigose	villous-sericeus	glabrous

species (contrary to the meaning of the generic name).

The five species have glandular corolla tubes with the trichomes, "g" in Table 1, being similar to those in *Chrysothamnus* (fig. 20–22, Anderson 1970a); however, those in *H. zionis* are less abundant, are longer, and have narrower glandular heads as in Figure 19. Additionally, corollas of *H. crispus* have a few very long, nonglandular villi like Fig. 17 of Anderson (1970a).

Nectaries at the base of the style are most prominent in *H. zionis* and least so in *H. crispus*. The new species have somewhat thicker corollas than do *H. bloomeri* and *H. suffruticosus* as determined by cell number radially through the tubes between adjacent vascular bundles.

Nodal anatomy is trilacunar, three trace for the species. In leaf anatomy, they are similar in that leaves are isolateral with three rows of palisade cells facing each epidermis. Bundle sheath extensions are present only on the midvein—a feature characteristic of all taxa of Haplopappus with a chromosome base of x = 9, whereas those with x = 4, 5, or 6 have leaves with bundle sheath extensions on lateral veins as well. A possible exception would be $H.\ parryi$, (x = 9 group), which has many bundle sheath extensions on bifacial leaves, but it is better placed in Solidago (Anderson and Creech 1975).

Some variation exists in leaf thickness. Of leaves studied, those of H. compactus and H. zionis have blades averaging 336 μ m thick with midveins 480 and 350 μ m, respectively. Leaves of H. crispus are thicker, 355 μ m in the blade and 400 at the midvein. Much thinner leaves occur in H. suffruticosus with blades 202 and 250 (Anderson 2970 and 2920, respectively), and both with midveins about 260 μ m thick.

Glandular trichomes on leaves of H. compactus and H. crispus average 77 µm long with nearly spherical heads 50 µm and 38 µm wide, respectively. Glands on H. zionis

Table 2. Features of floral anatomy for selected taxa of Haylonappus, section Macronema.

Taxon	Ovarian bundle number		Secretory canal distribution					
			Achene		Corolla			
	Average	Range	I	I1	III	IV	V	
H. bloomeri	5.5	5-6	+	+ +	+	+	+	
H. compactus	5.5	5-6	++	+ +	+ +	+ +	+	
H. crispus	5.0	5	+ +	+ +	0	+	++	
H. suffruticosus	5.2	5-6	+	+ +	+	+	_	
H. zionis	7.0	5-9	+	+	++	++	+	

leaves, though somewhat less abundant, have larger buttressed bases and average 100 $\mu \rm m$ long with heads 38 $\mu \rm m$ wide. For H. suffruticosus, glands on Anderson 2970 leaves average 80 $\mu \rm m$ long with spherical heads, whereas those on Anderson 2920 have long slender stalks and heads, averaging 220 $\mu \rm m$ long with the elongate heads 48 $\mu \rm m$ long and 29 $\mu \rm m$ wide. Glands on H. bloomeri are nearly sessile, only 38–42 $\mu \rm m$ long with spherical heads 29 $\mu \rm m$ in diameter.

RELATIONSHIPS

Table 2 gives ranges of the species and summarizes some aspects of their morphology based on my observations; some measurements differ from those of Hall (1928). Reveal 1070 is an unusual form of H. bloomeri, with exceptionally large heads with many long disk flowers (features listed parenthetically in Table 2).

The new species do not occur close geographically to *H. bloomeri* or *H. suffruticosus*, species with which they have been confused. Further, the new species are distinct from the other two in their constant absence of ray flowers. Ray flowers are almost

always present in heads of *H. bloomeri* and *H. suffruticosus*, and, although occasionally individual plants may be eradiate, some plants of the population will always have rays.

Haplopappus compactus, once considered a subspecies of H. bloomeri, differs from that species in involucral length and width, disk flower number, corolla shape, and achene size as well as the absence of ray flowers and some aspects of leaf shape and size. Haplopappus compactus and H. zionis appear to be closely related. Both have dilated corolla tubes. They can be distinguished in habit, head size, and style length, and generally so in leaf shape and size. In addition, H. zionis usually has leafier involucres. The two also differ anatomically.

Haplopappus crispus is intermediate geographically between H. compactus and H. zionis, but it is closer to H. suffruticosus in relationship even though it is eradiate. In addition to absence of rays, H. crispus can be further distinguished from H. suffruticosus by its habit, leaf size and thickness, degree of glandularity (and odor), narrower heads, fewer flowers, and sparsely strigose achenes.

A key to the new species and related taxa is presented here.

Table 2 continued.

		Trichomes				_ Corolla			Index of
Nectary length, μm	Achene		Corolla tube			thickness			
	Freq.	Length, mm	Туре	Freq.	Length, μm	A	В	С	specialization
144	_	0.5	g	++	150	7	5	2	6.5
168	_	0.43	g	+	168	8	5	2	5.6
115	+	0.53	g	++	165	7	6	2	6.8
			n	_	432				
140	++	0.8	g	++	160	7	5	2	6.9
240		0.52	g	_	270	8	6	2	5.0

In the Asteraceae, amounts of secretory tissue and floral venation bear evolutionary significance with a reduction in both usually indicating advancement. In *Chrysothamnus*, these features (correlated with other characteristics such as karyotypes) were used to develop a phylogenetic index of specialization on a scale of 0–10 for the taxa (Anderson and Fisher 1970).

Section Macronema is close to *Chrysothamnus* with natural hybridization known to occur between *H. macronema* and *C. nauseosus* (Anderson and Reveal 1966). Therefore, the index of specialization developed for *Chrysothamnus* should be applicable for showing relationships among the new species. Index values are listed in Table 2. Reduction in involucral bract vasculature is apparently correlated with that of the ovary wall; phyllaries of *H. zionis* have three vascular bundles each; those of *H. crispus* have one.

Of the taxa studied here and in Anderson (1970a), H. macronema (the most widespread species in the section) has the lowest index number of 4.5, and H. ophitidus (clearly a derived species that is specialized for serpentine) has the highest at 8.5. Hall (1928) considered H. suffruticosus the most primitive member of section Macronema, but H. macronema is probably a better candidate. Haplopappus compactus, and, especially, H. zionis, though much more restricted in range than H. bloomeri and H. suffruticosus, seemingly represent more primitive stock phylogenetically.

ACKNOWLEDGMENTS

Appreciation is expressed to Stanley L. Welsh for field trip support and to Wesley

Niles for seed of *H. compactus*. Melanie Darst prepared the line drawings; Walter Forehand is thanked for assistance with the Latin diagnoses. This study was supported by National Science Foundation Grant DEB 76–10768.

LITERATURE CITED

- Anderson, L. C. 1964. Taxonomic notes on the *Chrysothamnus viscidiflorus* complex (Astereae, Compositae). Madroño 17:222-227.
- _____. 1970a, Floral anatomy of *Chrysothamnus* (Astereae, Compositae). Sida 3:466-503.
 - _____. 1970b. Embryology of *Chrysothamnus* (Astereae, Compositae). Madroño 20:337-342.
- Anderson, L. C., and J. B. Creech. 1975. Comparative leaf anatomy of *Solidago* and related Asteraceae. Amer. J. Bot. 62:486–493.
- Anderson, L. C., and P. S. Fisher. 1970. Phylogenetic indicators from floral anatomy in *Chrysothamnus* (Astereae, Compositae). Phytomorph. 20: 112-118.
- Anderson, L. C., and J. L. Reveal. 1966. Chrysothamnus bolanderi, an intergeneric hybrid. Madroño 18:225–233.
- Anderson, L. C., D. W. Kynos, T. Mosquin, A. M. Powell, and P. H. Raven. 1974. Chromosome numbers in Compositae. IX. *Haplopappus* and other Astereae. Amer. J. Bot. 61:665-671.
- CLOKEY, 1. W. 1951. Flora of the Charleston Mountains, Clark County, Nevada. Univ. California Publ. Bot. 24:1-274.
- HALL, H. M. 1928. The genus *Haplopappus*, a phylogenetic study in the Compositae. Carnegie Inst. Publ. 389:1–391.
- Nelson, J. B. 1982. Floral anatomy of North American Haplopappus (Asteraceae): systematic considerations. Unpublished dissertation. Florida State Univ. Library, Tallahassee.